THE ORDOVICIAN TRIMERELLID BRACHIOPOD *EODINOBOLUS* FROM SOUTH-EAST ONTARIO

by B. S. NORFORD *and* H. MIRIAM STEELE

ABSTRACT. *Obolus canadensis* Billings, *Obolellina magnifica* Billings, and *Dinobolus erectus* Wilson are redescribed. The species are Wilderness (early Caradoc) in age. Rowell recently assigned all three species to *Eodinobolus* and chose *Obolellina magnifica* as the type species. The internal structures of the three species are described from silicified material. A hypothesis is presented for the mechanics of the opening and closing of the shell and requires articulation about a poorly defined hinge that is analogous in its position to that of the Class Articulata.

THE internal morphology of trimerellid brachiopods is very poorly known for the interiors of most described species are known only from internal moulds that poorly display the features of the posterior regions of the thick shells. The discovery of a silicified *Dinobolus* in northern British Columbia (Norford 1960) revealed an unusual form of articulation. The present contribution is part of a continuing attempt to find well preserved material of the various trimerellid genera, to fully describe the internal morphology in the family, and to assess the relations of the family to the rest of the phylum.

Three species of trimerellid brachiopods have been described from the Fourth Chute of the Bonnechere River and from Paquette Rapids on the Ottawa River, both in Renfrew County, south-east Ontario. All three species, *Obolus canadensis* Billings, *Obolellina magnifica* Billings, and *Dinobolus erectus* Wilson were recently placed in the genus *Eodinobolus* Rowell with *O. magnifica* chosen as the type species (Rowell 1963). The internal features were not adequately described although the type specimens of all three species are silicified.

Several large blocks of limestone were collected by the present authors and G. W. Sinclair from a thin stratigraphic interval at the Fourth Chute. The blocks, when etched, provided more than 300 trimerellid brachiopods.

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GEOLOGICAL SETTING

The Bonnechere outlier is one of several small outliers of Palaeozoic sediments on the Precambrian Shield in Renfrew County. At Fourth Chute, the Bonnechere River has cut a deep gorge through limestones that dip gently to the north and has exposed a section about 40 ft. thick (Kay 1942, more than 37 ft.; Barnes 1967, 33 ft.).

The specimens of *Eodinobolus* were collected from outcrops on both sides of the river at the top of the gorge and are from the uppermost 10 ft. of beds exposed at Fourth Chute (GSC. Locality 73484). Except for two shells of *E. canadensis*, all the valves of *Eodinobolus* are disarticulated and most are broken. The thick posterior regions of the

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platforms of the brachial valve of *E. magnificus* are common as separate fragments. These are strong remnants of shells that were broken by wave action or by the winnowing of vigorous currents. The limestones at the collecting locality are yellowish-brown calcarenites with abundant biogenic fragments. Clear calcite is present both as cement and as fine stringers. Residues insoluble in hydrochloric acid contain common fine quartz sand and light brown clay-size material. Flattened ropey masses of impure chert are common and silicified fossils are locally abundant in layers and pockets.

Resistant thick beds of similar rock to that of the collecting locality form most of the section at the Fourth Chute but chert is only common in the uppermost beds. Three minor intervals of very thinly bedded, very pale grey limestones are present within the sequence. Kay (1942, pp. 595–6, 601, 604) recognized 37 ft. of Chaumont beds in the lower part of the gorge and assigned the overlying beds that include the present collecting locality to the Rockland Formation. Recently Barnes (1967, p. 216) continued Kay's usage but referred the basal beds of the section to the Lowville Formation. Wilson (1946, pp. 10, 16–17) assigned collections from Fourth Chute to the Leray–Rockland beds of the Ottawa Formation. Fossils are only abundant at the top of the gorge and these collections can be assumed to be from the same uppermost beds as Locality 73484. Satterly (1945) mapped the rocks as Ordovician without attempting assignment to a formation. Application of the term Chaumont in the Ottawa Valley is not widely accepted and the Rockland Formation should probably be used for the whole sequence at Fourth Chute (Sinclair, personal communication).

The blocks of rock of the fossil collections were selected primarily for specimens of *Eodinobolus* and the following fauna recovered by etching may not be completely representative of the fauna of the beds.

Eodinobolus canadensis (Billings), *E. erectus* (Wilson), *E. magnificus* (Billings), *Eichwaldia subtrigonalis* Billings, *E. tricenaria* (Conrad), *Idiospira panderi* (Billings), *Oepikina* sp., *Rafinesquina* sp., *Strophomena* sp., *Ctenodonta nasuta* (Hall) sensu Salter, *C. logani* Salter, *Cyrtodonta* sp., *Lyrodesma acuminatum* Ulrich sensu Wilson, *Tancrediopsis* '*abrupta*' (Billings), *T. contracta* (Salter), '*Cycloceras*' *cylindratum* Foerste, *Michelinoceras* sp., '*Spyroceras*' sp., *Richardsonoceras* sp., *Ectomaria pagoda* (Salter), *Eunema strigillata* Salter, *Helicotoma planulata* Salter, *Hyolithes* sp., *Hormotoma* sp., *Lophospira perangulata* (Hall), *Maclurites logani* (Salter), ? *Trochonema* sp., *Tropidodiscus* (?) *argo* (Billings), *Receptaculites* sp., stromatoporoid, *Calapoecia* sp., *Lambeophyllum* sp., *Streptelasma* sp., bryozoans, echinoderm fragments.

Many of these species are also found at Paquette Rapids, Ontario and Quebec (Kay 1942, pp. 602–3), where about 20 ft. of the Rockland Formation are exposed in another small outlier. The holotype and paratypes of *Eodinobolus magnificus* were collected at Paquette Rapids. The Fourth Chute and Paquette Rapids faunules are coeval and are within the Wilderness Stage of Cooper (1956, pp. 8–9). The Wilderness largely corresponds to the Black River interval of earlier usage and can be correlated within the lower part of the Caradoc Stage of the Welsh Borderland.

The specimens of *Eodinobolus* are coarsely silicified but very fragile. Adherent adventitious material is difficult to remove without damaging the shells. Fortunately many specimens are available and composite descriptions of the morphology of the species are possible. All known specimens of the species are in the collections of the Geological Survey of Canada, Ottawa, except for four specimens of *Eodinobolus magnificus* that are in the United States National Museum, Washington.

SYSTEMATIC PALAEONTOLOGY

Phylum BRACHIOPODA
Family TRIMERELLIDAE Davidson and King 1872
Genus EODINOBOLUS Rowell 1963

1963 *Eodinobolus* Rowell, pp. 37–9.
1965 *Eodinobolus* Rowell; Rowell, p. H274.

Type species. *Obolellina magnifica* Billings 1872, from the Rockland Formation at Paquette Rapids on the Ottawa River, Ontario and Quebec.

Diagnosis. (Rowell 1963, p. 37); 'Early trimerellids. Elongate oval to transversely oval in outline. Gently biconvex. Pseudo-interarea of ventral valve relatively low, triangular. Muscle platforms in both valves approximately diamond shaped in outline, very low, particularly in the dorsal valve, solid, not elevated anteriorly or excavated. Median ridges poorly developed or absent. Ventral beak solid.

Differs from all later trimerellids in the poor development of the muscle platforms.'

Discussion. Rowell discovered that the genus *Obolellina* was a junior objective synonym of *Rhynobolus* and essentially proposed *Eodinobolus* to provide a valid generic name for several early trimerellid species that had been previously assigned to *Obolellina*. The present authors have studied only the three species from the Rockland Formation. Published descriptions of the other species assigned to *Eodinobolus* (Rowell 1963, p. 39) lack sufficient detail of internal morphology to allow fruitful comparison with the type species of the genus. The pedicle valves of the three Rockland species are broadly similar but the brachial valve of *canadensis* is strikingly different from those of *magnificus* and *erectus*. The differences may warrant generic differentiation but proposal of new genera of trimerellid brachiopods seems to be premature when so little is known of the morphology of the existing genera. For the present, *canadensis* is retained within *Eodinobolus*.

The terminology used in the description of the species is based, with minor modifications, on the usage evolved by Davidson and King (1874), Norford (1960), and Rowell (1965). Several scars can be differentiated on the interiors of the valves and are assumed to be the sites of muscle attachment. The pattern of scars is much better known than in *Dinobolus* or any other genus of the family but the relations between the scars of the two valves cannot yet be unequivocally demonstrated.

Opening and closing of shell. The mechanics of opening and closing of the shell in the trimerellid brachiopods are not fully understood. The form of the forward edge of the homeochilidial plate of the brachial valve of *Eodinobolus* and of the cardinal socket of the pedicle valve would not have allowed any lateral movement of the valves relative to each other, although some forward and rearward sliding might have been possible. A small amount of movement perpendicular to the commissure seems very likely. Simple dorsal-ventral movement of the whole brachial valve towards and away from the pedicle valve may be postulated. Closing of the shell would be achieved by contraction of all the muscles, but the problem of a mechanism of opening the shell cannot be readily resolved.

A hypothesis of opening and closing of the shell by means of rotation of the brachial valve about a static axis is shown by text-fig. 2. *Eodinobolus canadensis* is illustrated because the pseudo-interarea of its brachial valve is less modified and reduced than those of *E. magnificus* and *E. erectus*. A likely axis would be between the antero-lateral corners of the propareas of the pedicle valve; in the brachial valve, the corresponding line would lie near the rear parts of the postero-lateral grooves (points *a* in text-fig. 2). With such an interpretation, the valves could be opened by the contraction of a set of three muscles lying behind this line and pulling directly between the valves (text-fig. 2B). These muscles were attached to the pedicle valve at the front of the median part of the cardinal socket and to a pair of short scars lying lateral to the rear of the cardinal buttress; this pair is not discernible in the type species but can be seen in *E. canadensis* and *E. erectus* (text-figs. 1D, F). In the brachial valve, these muscles were attached to three scars just in front of the forward edge of the homeochilidial plate. A less likely possibility is that the scars in the pedicle valve belong to minor muscles and that the set in the brachial valve are those of adductors rooted somewhere on the platforms of the pedicle valve. In either case the valves could be closed by the contraction of muscles attached to the large scars on the muscle platforms and pulling directly between the valves. A slight rearward gape was probably present between the edge of the homeochilidial plate and the cardinal socket when the shell was closed (text-fig. 2A). This gape would be closed when the valves were open (as in *E. magnificus*, Pl. 32, fig. 11) and it is difficult to imagine a functional pedicle passing between the valves. In the valve-open position (text-fig. 2B), the concave homeodeltidium would closely mould the main part of the homeochilidial plate and the umbo of the brachial valve. The brachial valve of *E. canadensis* has a longer pseudo-interarea than the other two species and, as would be expected from the hypothesis, the pedicle valve has a deeper and more concave homeodeltidium. This form of articulation would not be very different from that of the Articulata but in that class the hinge consists basically of a pair of specialized hinge teeth in the pedicle valve and corresponding sockets in the brachial valve. The corresponding sites in the pedicle and brachial valve of *Eodinobolus* show no such specialization and one can assume that the articulation was inefficient and the amount of possible movement small. However, the approximate location at which one would look for a tooth and socket articulation is the site of the rear parts of a pair of deep grooves in both valves, postero-lateral to the platforms. Possibly these grooves accommodated a pair of strong muscles that acted as the actual pivots of the valves.

This hypothesis is tenable for the three described species of *Eodinobolus* and probably also for the Silurian *Dinobolus* cf. *D. conradi* (Hall) from northern British Columbia (Norford 1960, 1962). However, it can only be regarded as tentative until other genera of the trimerellids are as well known as *Dinobolus* and *Eodinobolus*. The various genera of the family have many bizarre features in common and it is reasonable to assume that they all opened and closed their shells in the same manner.

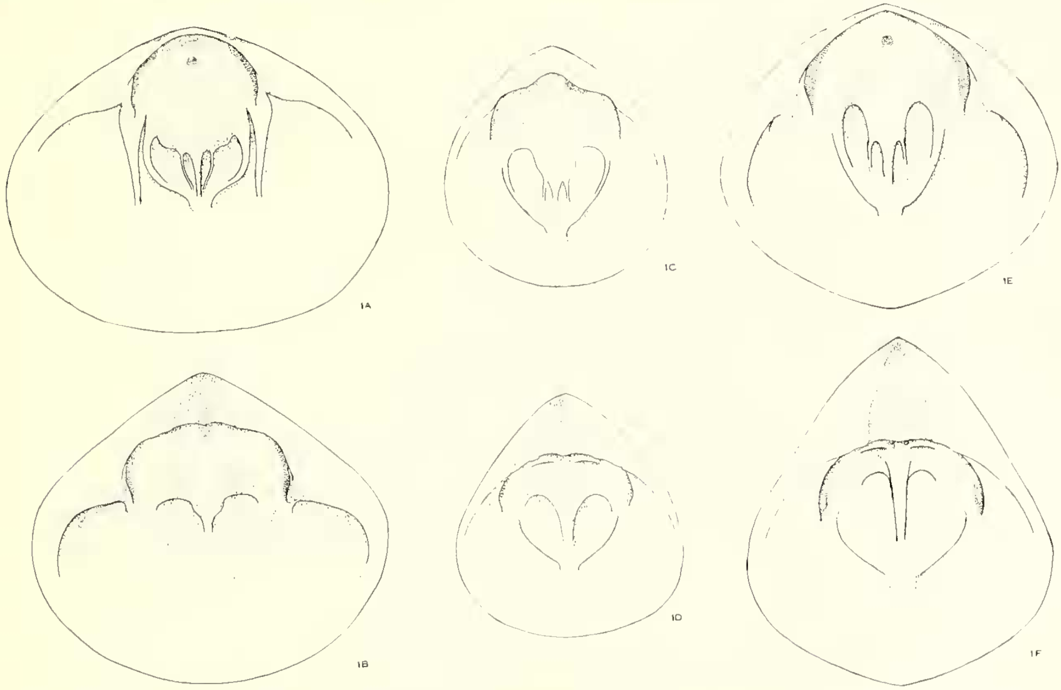
Eodinobolus magnificus (Billings, 1872)

Plate 32, figs. 1–26; text-figs. 1A, B

1858*a* *Obolus canadensis* Billings (pars), fig. 19.
1858*b* *Obolus canadensis* Billings (pars); Billings, fig. 19.
1872 *Obolellina? magnifica* Billings, pp. 329–30, fig. 8.
1874 *Dinobolus magnificus* (Billings); Davidson and King, pp. 126, 164, pl. 19, fig. 8.
1875 *Dinobolus magnificus* (Billings); Nicholson, p. 18 (*non* fig. 6*a*).
1946 *Dinobolus magnificus* (Billings); Wilson, p. 17, pl. 1, figs. 26, 27.

1956 *Obolellina magnifica* Billings; Cooper, pp. 231–2, pl. 13, figs. 1–3; pl. 24, fig. 25.
1963 *Eodinobolus magnificus* (Billings); Rowell, pp. 37, 39.
1965 *Eodinobolus magnificus* (Billings); Rowell, p. H274, fig. 169, 3*a–c*.

Material. Holotype GSC 1161, a brachial valve collected by Billings from Paquette Rapids. Paratypes, all from Paquette Rapids: GSC 1161a, the apical part of a shell, fragments of both valves preserved, GSC 1161b, 1161c, 1161d, all brachial valves. USNM 116800a, 116800b, 116800c, 116800d, and two other valves, collected by G. W. Sinclair from GSC Loc. 77101, an old quarry in the Rockland Formation on the south side of the Bonnechere River, a mile below Eganville. 87 brachial valves and 40 pedicle valves from GSC Loc. 73484 at Fourth Chute, including GSC 22930–41.



TEXT-FIG. 1. Diagrams of the internal features of *Eodinobolus*; magnifications $\times 1\frac{1}{2}$. A, B. The type species *Eodinobolus magnificus* (Billings), brachial valve and pedicle valve. C, D. *Eodinobolus canadensis* (Billings), brachial valve and pedicle valve. E, F. *Eodinobolus erectus* (Wilson), brachial valve and pedicle valve; platform and cardinal buttress shown in text-fig. 1F based on developments in a small specimen (GSC 22942).

Description. Shell thick, large, biconvex with brachial valve probably about twice as deep as pedicle valve. Outline suboval with flattened front, slightly wider than long, greatest width at about mid-length. Anterior commissure very faintly uniplicate, lateral commissures plane. Ornament of widely spaced growth-lines on exteriors, rare specimens show growth-lines on interiors of valves; numerous closely spaced faint growth-lines visible on pseudo-interareas of large individuals.

Pedicle valve shallow, greatest depth a little behind mid-length, beak small, slightly incurved, apical angle of shell about 100–115°. Pseudo-interarea large, moderately long, orthocline, gently concave, with depressed concave homeodeltidium indistinctly set off from the bordering propareas, except in a few large individuals (Pl. 32, fig. 18). Pair of widely divergent grooves limit propareas, very indistinct in most specimens but marked in some (Pl. 32, fig. 18). No pedicle opening. The front half of the homeodeltidium in the sole specimen in which both valves are preserved (Pl. 32, figs. 8–11) bears what may be the remnants of a low semiconical plate or pair of plates, the base of which abuts against the beak of the brachial valve in the interpreted valve-open position (text-fig. 2B and Pl. 32, fig. 11), but would have been apart from it in the valve-closed position (text-fig. 2A). This structure might be interpreted as a pedicle sheath but appears to be cut off from the shell's interior by the homeochilidial plate of the brachial valve (Pl. 32, fig. 11). No other pedicle valves show any traces of this structure. Hinge plate low, indistinct, without umbonal chambers, posterior part without a cardinal buttress but with a short shallow wide depressed transverse area, the cardinal socket (Pl. 32, figs. 14, 15, 19). Platform wide, reaching forward to about mid-length, resting directly on floor of valve; very faint in small specimens, indistinct in those of average size, but distinct and with thickened posterior regions in large specimens (Pl. 32, figs. 15, 18); front and lateral margins gently rounded; front half of platform with low median septum corresponding in position to cardinal buttress and dividing a pair of broad shallow scars. No distinct scars visible on floor of valve outside front part of platform, a pair of deep grooves border postero-lateral parts of platform.

Brachial valve wider than long, moderately deep, greatest depth just behind mid-length; beak minute. Pseudo-interarea almost obsolete, rear margin of valve basically consisting of a strong high gently curved transverse edge (of the extremely short homeochilidial plate) articulating with the cardinal socket of the pedicle valve, together with a pair of small depressed transverse areas behind and outside the edge (Pl. 32, figs. 7, 22). Set of three shallow impressions present on hinge plate in front of homeochilidial plate (Pl. 32, figs. 21, 22, 26), lateral pair wider and slightly further forward than median impression, which itself may be axially divided. Platform strongly developed, longer than wide, resting directly on valve floor, extending forward well beyond mid-length, with rounded but irregular lateral and front margins, rear parts of platform greatly thickened in large specimens (Pl. 32, figs. 23–6). Front third of platform bears seven raised septa separating muscle scars (Pl. 32, figs. 7, 22, 26). Inner two pairs of lateral septa curve

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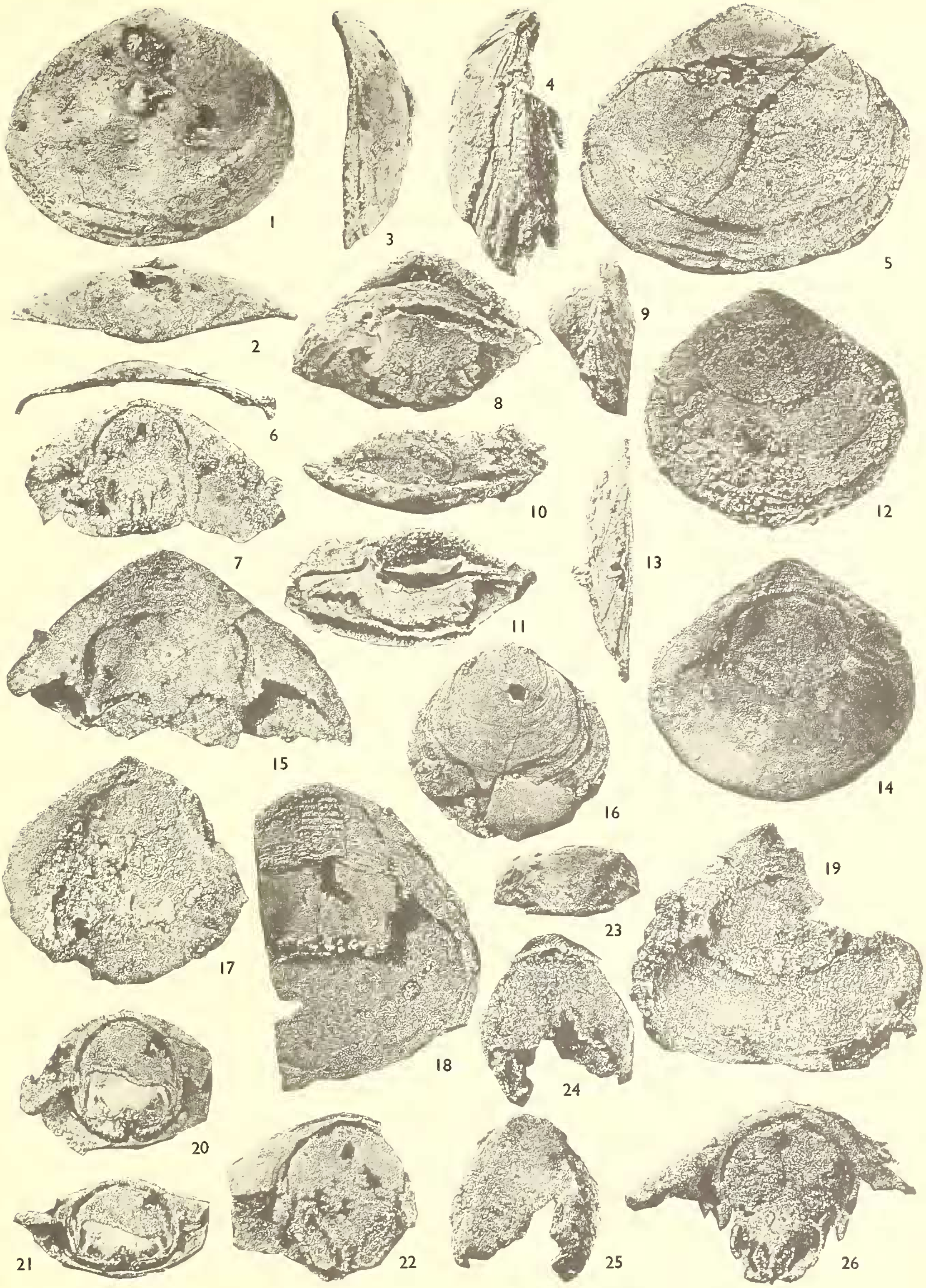
EXPLANATION OF PLATE 32

All figures natural size. All specimens from the Rockland Formation of south-east Ontario and unless otherwise indicated, from GSC Loc. 73484, Fourth Chute of the Bonnechere River.

Figs. 1–26. *Eodinobolus magnificus* (Billings). 1–3. External, rear, and lateral views of the holotype brachial valve (GSC 1161); from Paquette Rapids. 4, 5. Lateral and external views of a large brachial valve (GSC 22930). 6, 7. Rear and internal views of a brachial valve (GSC 22931). 8–11. Brachial, lateral, rear, and front views of a fragmentary paratype (GSC 1161a) in which the two valves are still in living position; from Paquette Rapids. In fig. 11, the brachial valve is above and the front edge of its homeochilidial plate rests directly in contact with the cardinal socket on the floor of the pedicle valve; an unetched piece of limestone is present on the left side of the specimen. 12–14. External, lateral, and internal views of a pedicle valve (GSC 22932). 15. Internal view of a large pedicle valve (GSC 22933). 16. External view of a small pedicle valve (GSC 22934). 17–19. Internal views of small, large, and medium-sized pedicle valves (GSC 22935, 22936, 22937). 20, 21. Internal views of the rear part of a brachial valve (GSC 22938); strongly tilted in fig. 21. 22, 26. Internal views of medium-sized and large brachial valves (GSC 22939, 22940). 23–5. Rear, internal, and external views of a detached muscle platform (GSC 22941) from a brachial valve.



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axially to join with median septum and form an anterior limit to platform. Outer pair trend almost straight, but forward ends twist laterally just before dying out. Inner pair of scars very small, second pair much larger and more pronounced, outer pair long and narrow, a further pair of scars may be present outside outermost platform septa. Rear of platform bears a very deep narrow axial trench that starts abruptly some distance in front of homeochilidial plate and gradually fades away before mid-length of platform; this trench is normally pronounced but is faint in some specimens (Pl. 32, figs. 20, 25). Platform bounded postero-laterally by a pair of deep grooves. Low raised area trends forward a short distance from central part of front of platform. A few specimens show faint coarse pits just in front of shoulders of valve.

Discussion. Variation within the species seems to be primarily related to growth. Most large specimens have greatly thickened platforms, brachial pseudo-interareas, and shoulders of valves.

Eodinobolus canadensis (Billings, 1858)

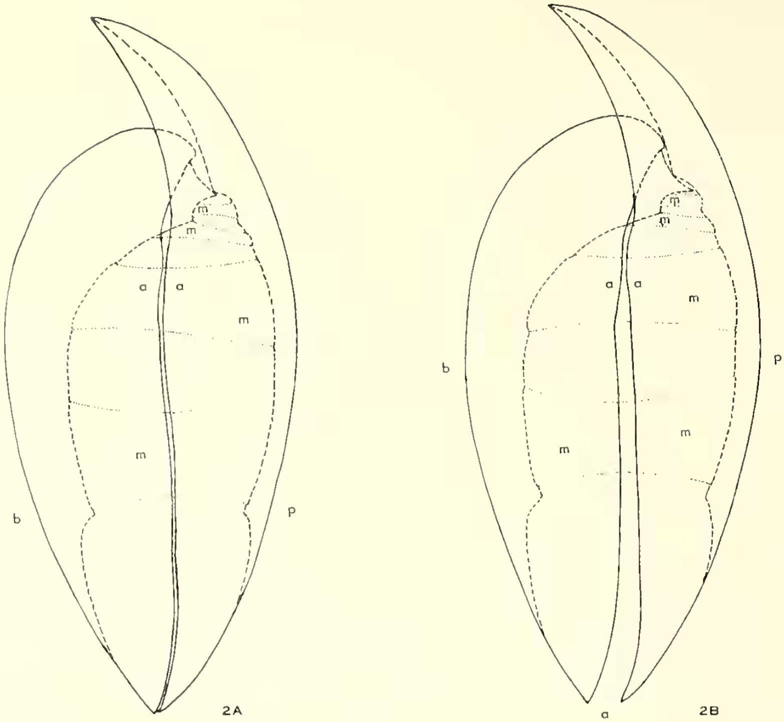
Plate 33, figs. 1–28; text-figs. 1C, D, 2

1858*a* *Obolus canadensis* Billings, pp. 189–90, figs. 20–3 (*non* fig. 19).
1858*b* *Obolus canadensis* Billings; Billings, pp. 441–2, figs. 20–3 (*non* fig. 19).
1863 *Obolus canadensis* Billings; Logan *et al.*, p. 942, fig. 75*a–c*, *non d*.
1871 *Obolellina canadensis* (Billings); Billings, p. 222.
1872 *Obolellina canadensis* (Billings); Billings, pp. 327–8, figs. 1–5.
1874 *Dinobolus canadensis* (Billings); Davidson and King, pp. 126, 162–3, pl. 19, fig. 7.
1946 *Dinobolus canadensis* (Billings); Wilson, p. 16, pl. 1, fig. 24.
1956 *Obolellina canadensis* (Billings); Cooper, p. 230, pl. 24, fig. 24.
1963 *Eodinobolus canadensis* (Billings); Rowell, p. 39.

Material. Holotype GSC 1150, a complete specimen collected by Billings from the Fourth Chute of the Bonnechere River, the same locality and almost certainly the same horizon as GSC Loc. 73484. Paratypes GSC 1150b, 1150c, 1150d, brachial valves, and 1150a, a small complete specimen; all from the same locality as the holotype. 89 brachial valves and 128 pedicle valves from GSC Loc. 73484 at Fourth Chute, including GSC 22943–56.

Description. Shell thick, biconvex with depth of pedicle valve about two-thirds that of brachial valve. Outline suboval, large shells slightly longer than wide, small shells equidimensional, greatest width just in front of mid-length. Anterior commissure rectimarginate, lateral commissures plane. Ornament of widely spaced growth-lines on exterior; numerous closely spaced faint growth-lines on pseudo-interareas.

Pedicle valve shallow, greatest depth at about mid-length; small, strongly incurved beak, apical angle of shell about 85–105°. Pseudo-interarea large, long, gently anacline, concave; with prominent concave homeodeltidium that is distinctly set off from bordering propareas. Pair of widely divergent shallow grooves limiting propareas on pseudo-interareas, situated about midway between homeodeltidium and lateral margins (Pl. 33, figs. 24, 25). No pedicle opening. Hinge plate thick, without umbonal chambers, supported by very low coarse cardinal buttress that tapers and becomes indistinct forward without quite reaching front of platform. Rear part of hinge plate bears a wide shallow depressed transverse area, the cardinal socket (Pl. 33, figs. 24, 27). Platform wide, reaching beyond mid-length, resting directly on floor of valve, with almost straight antero-lateral margins, front medianly thickened and elevated, and in front of platform, a low



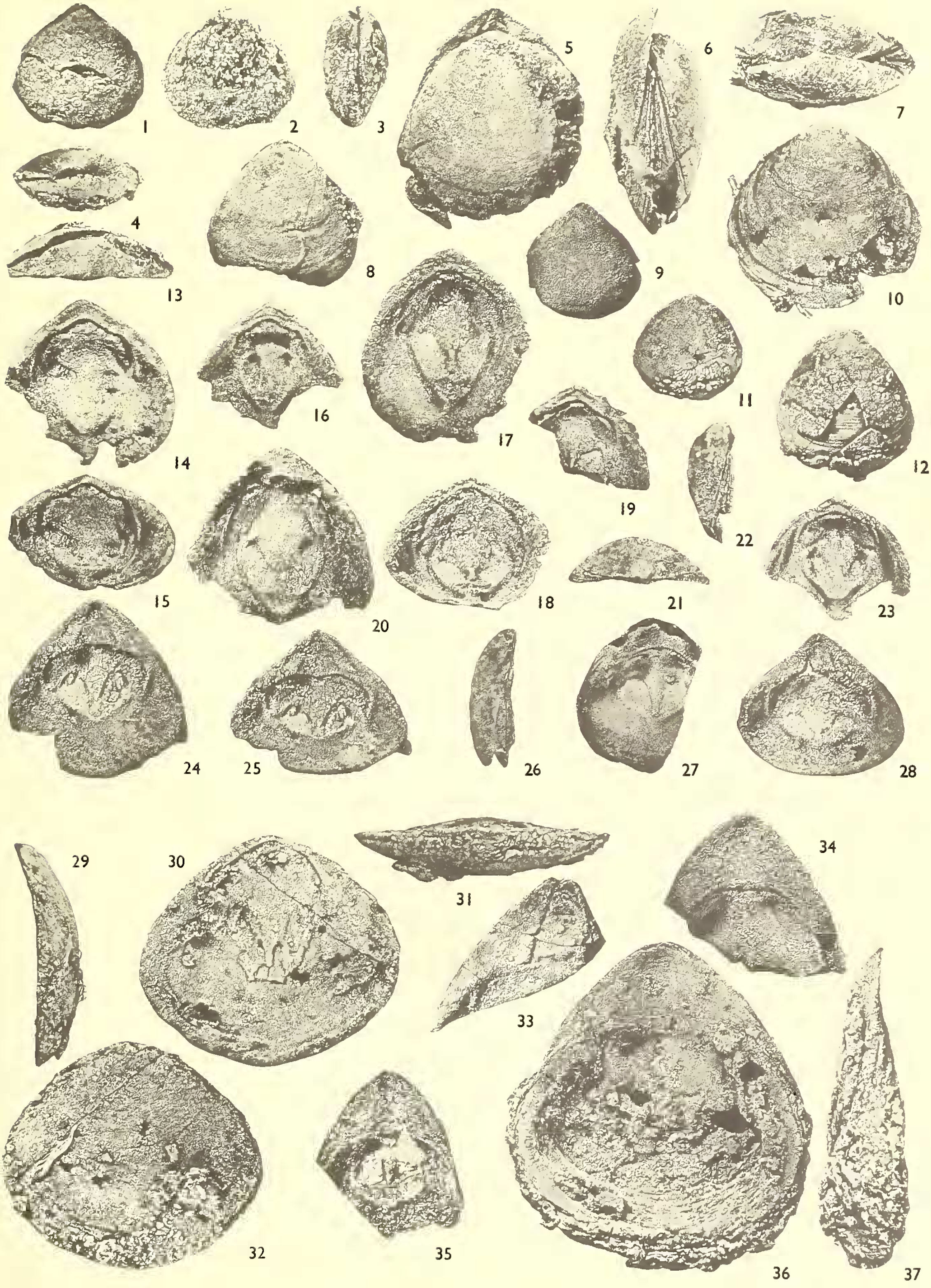
TEXT-FIG. 2. Hypothesis for opening and closing of shell of *Eodinobolus canadensis* (Billings), involving relaxation and contraction of muscles and rotation about an axis through *aa* and perpendicular to the plane of the diagram; *a* (unspecialized hinge area in each valve); *p*, pedicle valve; *b*, brachial valve; *m*, muscle; *o*, gape; magnification about ×3. A. Shell closed, note possible small gape at rear of shell in shell-closed position; shell can be opened by contraction of muscles to rear of *aa* and relaxation of large muscles on muscle platforms in front of *aa*. B. Shell open; shell can be closed by contraction of large muscles on muscle platforms in front of *aa* and relaxation of muscles to rear of *aa*.

EXPLANATION OF PLATE 33

All figures natural size. All specimens from GSC Loc. 73484, Rockland Formation, Fourth Chute of the Bonnechere River, south-east Ontario.

Figs. 1–28. *Eodinobolus canadensis* (Billings). 1–4. Brachial, pedicle, lateral, and rear views of a paratype (GSC 1150a). 5–7. Brachial, lateral, and rear views of the holotype (GSC 1150). 8, 10–12. External views of pedicle valves (GSC 22944, 22946, 22947, 22945). 9. External view of a brachial valve (GSC 22943). 13–15. Rear, internal, and tilted internal views of a brachial valve (GSC 22948). 16, 22. Internal and lateral views of a brachial valve (GSC 22949). 17–20. Internal views of brachial valves (GSC 22952, 22951, 22956); fig. 18 is a tilted view of the specimen shown in fig. 17. 21, 23. Rear and internal views of a brachial valve (GSC 22950). 24–6. Internal, tilted internal, and lateral views of a pedicle valve (GSC 22953). 27, 28. Internal views of pedicle valves (GSC 22954, 22955); fig. 28 shows a tilted valve.

Figs. 29–37. *Eodinobolus erectus* (Wilson). 29–32. Lateral, internal, front, and external views of a brachial valve (GSC 22957). 33, 34. Internal views of the rear parts of two fragmentary pedicle valves (GSC 22958, 22959). 35. Internal view of a small pedicle valve (GSC 22942). 36, 37. Internal and lateral views of the holotype pedicle valve (GSC 6301).



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